Haruki HIRABAYASHI*: **Chromosome numbers in Japanese species of *Dryopteris*** (3)

平林春樹*: 日本産オシダ属の染色体数 (3)

This paper is a continuation of the previous report in this Journal (1966, 1967). Materials employed and results obtained in the present study are shown in Table 1. In this table, the order of arrangement of taxa conforms to the classification by H. Ito (1939) and the mark ※ represents the specimen cultivated in Koishikawa Botanical Garden of University of Tokyo.

The author wishes to express his cordial thanks to Prof. H. Ito, Tokyo University of Education, for his helpful guidances and suggestions throughout the study and for his valuable comments on the manuscript and to Prof. S. Kurata, University of Tokyo, for his valuable advices during this work, and also for his kind supplies of materials without which the investigation could not have been made.

Notes *Dryopteris lacera* O. Kuntze form. *intermedia* H. Ito was proposed by H. Ito (1939) for a fern, considered as the hybrid between *D. lacera* O. Kuntze (n=41) and *D. uniformis* Makino (n=82). The hybridity of this plant was supported cytologically by Mitui (1967). He reported that the hybrid *D. lacera*×*uniformis* is an autotriploid and these compose an autopolyploid series. In the present study, the author also observed that this hybrid is triploid (2n=123), with approximately 41 bivalents and 41 univalents without trivalent pairing during meiosis.

Both *D. hangchowensis* Ching and *D. tasiroi* Tagawa (=*D. handeliana* C. Chr.) are diploid, each showing 41 bivalents at meiosis and are sexual, each producing 64 spores in sporogenesis (Fig. 1-A). *D. hangchowensis* was described originally by Kurata (1966) and this species is native in Japan, but it is very rare and local. *D. tasiroi* occurred in Japan was given the first description by Tagawa (1940) and this is also local in Japan. It is noticeable that each of these non-widespread species is a sexual diploid.

D. tokyoensis C. Chr. is diploid with n=41 and sexual with normal spore

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Table 1. The chromosome numbers in *Dryopteris*.

Sect.	Subsect.	Species	Chromosome number	Polyploidy, hybrid & reproduction	Locality
Eudryopteris	Dichasium	*D. lacera* form. *intermedia* Ainokokumawarabi	2n=123 meiosis irreg.	tripl. hybr.	Ongata, Tokyo Pref.※
	Cycadinae	*D. hangchowensis* Kirisimaiwahego	n=41	sexual dipl.	Miike, Kirisimayama, Miyazaki Pref. coll. by M. Kido※
		D. tasiroi (=*D. handeliana*) Tukusiokuzyaku	n=41	sexual dipl.	Namera, Sabagun, Yamaguti Pref. coll. by M. Yamasita※
		D. tokyoensis Tanihego	n=41	sexual dipl.	Nobeyama, Nagano Pref.
		D. commixta Tukusiiwahego	n=82	sexual tetrapl.	Tokka, Inasa, Sizuoka Pref. coll. by K. Satake※
		D. dickinsii Okuzyakusida	n=82	apog. dipl.	Kamikobayasi, Gotenba, Sizuoka Pref.※
		D. pycnopteroides Wakanasida	n=82	apog. dipl.	Miike, Kirisimayama, Miyazaki Pref.※
		D.×*hisatsuana* Hisatuokuzyaku	2n=82 meiosis irreg.	dipl. hybr.	Nokeebosi, Yamaemura, Kumamoto Pref.※
		D. kominatoensis Tanihegomodoki	2n=82 meiosis irreg.	dipl. hybr.	Ure, Aiti Pref.※
		D.×*hakonecola* Hakoneokuzyaku	2n=164 meiosis irreg.	tetrapl. hybr.	Kamikobayasi, Gotenba, Sizuoka Pref.※
		D. mayebarae Iwahegomodoki	2n=164 meiosis irreg.	tetrapl. hybr.	Tokka, Inasa, Sizuoka Pref. coll. by K. Satake※
		D. otomasui Yatakeiwahego	2n=164 meiosis irreg.	tetrapl. hybr.	Yatake, Masakimura, Miyazaki Pref.※
		D.×*pseudo-commixta* Osumiiwahego	2n=164 meiosis irreg.	tetrapl. hybr.	Takeno, Takakumayama, Kagosima Pref.※
	Monticolarum	*D. monticola* Miyamabenisida	n=41	sexual dipl.	Akagisan, Gunma Pref.※
	Pycnopteris	*D. sieboldii* Omitude (Nagasakisida)	n=82	sexual tetrapl.	Kyushu※
Nephrocystis		*D. hayatai* Inutamasida	n=41	sexual dipl.	Nagata, Yakusima※
		D. melanocarpa Kurominoitatisida	n=123 (two phases)	apog. tripl.	Hanaze, Tasiromura, Kagosima Pref.※
		D. yakusilvicola Kosugiitatisida	n=123	apog. tripl.	Kosugidani, Yakusima※
Polystichodrys	Erythro-variae	*D. erythrosora* var. *koidzumiana* Hokozakibenisida	n=41	sexual dipl.	Yakusima※
		D. gymnophylla Sakuraikaguma	n=41	sexual dipl.	Agano, Saitama Pref.
		D. sordidipes Yogoreitatisida	n=41	sexual dipl.	Yakusima※
		D. kenzoi (named temporarily by Kurata) Ensyubenisida	n=123	apog. tripl.	Sizuoka Pref. coll. by K. Satake※
		D. labordei var. *simasakii* form. *paleacea* Atuginonuka-itatisidamagai	n=123 (two phases)	apog. tripl.	Inuyama, Aiti Pref.※
		D. sacrosancta Himeitatisida	n=123 (two phases)	apog. tripl.	Owase, Mie Pref.
		D. ryo-itoana Owasebenisida	n=123	apog. tripl.	Kinkasan, Gihu Pref.※
	Formosanae	*D. formosana* Takasagosida	n=123	apog. tripl.	Miyakoda, Hamamatu, Sizuoka Pref.※
Lophodium	Austriacae	*D. austriaca* Siranewarabi	n=41	sexual dipl.	Yasyazintoge, Yamanasi Pref.

formation as Kurita (1961) reported previously.

D. commixta Tagawa is tetraploid with n=82 and is sexual, producing 64 spores in a sporangium (Fig. 1-D). This agrees with the previous report by Kurita (1967).

Both *D. dickinsii* C. Chr. and *D. pycnopteroides* C. Chr. are diploid, each showing 82 pairs during meiosis and probably apogamous, for 32 spores are produced in each sporangium (Fig. 1-F). Mitui (1965) and Kurita (1965) reported the number n=82 and suggested apogamous reproduction in *D. dickinsii.* Momose (1967) described the presence of apogamy for the lack of archegonium formation in *D. pycnopteroides* and suggested the presence of apogamy for the structure on neck of archegonium in *D. dickinsii.*

D.×hisatsuana Kurata was proposed by Kurata (1964) for a fern, considered as the hybrid between *D. handeliana* C. Chr. (=*D. tasiroi* Tagawa) and *D. lacera* O. Kuntze. The type specimen of this plant, from cytological investigation by the author, showed lack of chromosome pairing and gave a chromosome count of 82 singles during meiosis, indicative of hybridity. Since both *D. handeliana* and *D. lacera* are fertile species having 41 gametic chromosome numbers, it supports cytologically the proposition by Kurata. Additionally, most of spores of this plant are abortive, although it has 16 spore mother cells in the sporogenesis.

D. kominatoensis Tagawa, on the basis of morphology, is an intermediate between *D. tokyoensis* C. Chr. and *D. monticola* C. Chr. Cytological investigation by Kurita (1961, 1965) showed that *D. kominatoensis* is a diploid with 2n=82 and both *D. tokyoensis* and *D. monticola* are a diploid with n=41. He suggested that *D. kominatoensis* is a hybrid between these two species. The author also observed in the present study that *D. kominatoensis* is a diploid, 2n=82, with complete failure of pairing or occasionally a few loosely connected pairs at meiosis, indicative of hybridity (Fig. 1-C). In addition, this plant shows 16 spore mother cells, but the spores are various in size and probably in fertility.

D.×hakonecola Kurata was proposed by Kurata (1958) for a fern, considered as the hybrid between *D. dickinsii* C. Chr. and *D. uniformis* Makino. This hybrid, from cytological investigation by the author, is tetraploid, 2n=164, with a degree of chromosome pairing at meiosis which is indicative of the genetic relationship between the tetraploid parental species. In a speci-

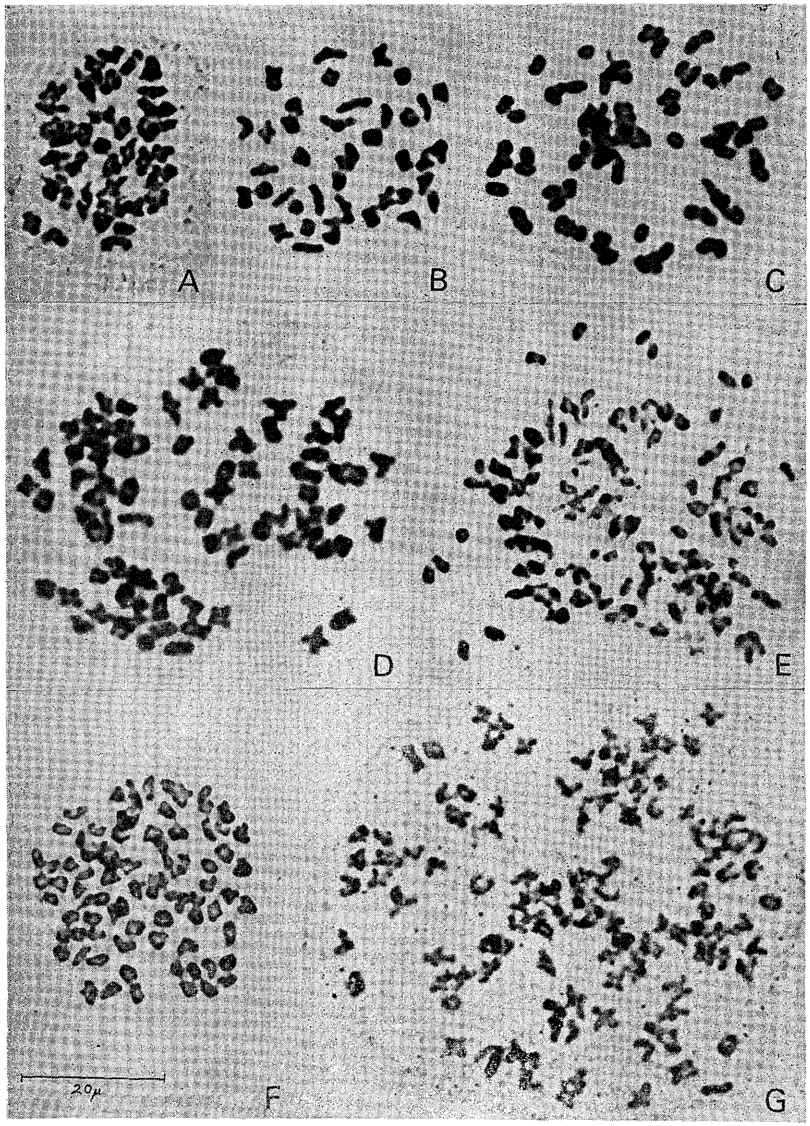

Fig. 1. Photomicrographs of chromosomes at meiosis. A. *D. hangchowensis* Ching n=41. B. *D. hayatai* Tagawa n=41. C. *D. kominatoensis* Tagawa 2n=82. E. *D.×pseudo-commixta* Kurata 2n=164. F. *D. pycnopteroides* C. Chr. n=82. G. *D. yakusilvicola* Kurata n=123.

men, it shows c. 32 pairs and c. 100 singles during first meiotic metaphase. *D. uniformis* is a sexual tetraploid species, with n=82. *D. dickinsii* may be apogamous diploid species as described above. Therefore, it seems that *D. hakonecola* results from to combine female gamete of *D. uniformis* with male gamete of *D. dickinsii*. These are able to support the proposition by Kurata. Additionally, this plant has normal 16 spore mother cells in a sporangium, but the spores are various in size and probably in fertility.

D. mayebarae Tagawa was named by Tagawa (1938) and proposed by Kurata (1958) as the hybrid between *D. commixta* Tagawa and *D. uniformis* Makino. Cytological investigation by Kurita (1967) in this hybrid, showed 2n=164, with many univalents and some bivalents (in a specimen, c. 86 univalents and c. 39 bivalents). In the present study, the author also observed 2n=164, with approximately 38 pairs and 88 singles during meiosis, indicative of tetraploid hybrid. The spore of this plant is abortive.

D. otomasui Kurata was described originally by Kurata (1967), as a fern having intermediate characteristics between *D. commixta* Tagawa and *D. polylepis* C. Chr. According to Kurata (1967), at the habitat of this plant, however, *D. commixta* appears but *D. polylepis* does not. Therefore, a putative parent of this hybrid is undetermined until now. Cytological study of the type specimen of this plant shows it to be tetraploid (2n=164) with a meiotic chromosomal arrangement of approximately 37 pairs and 90 singles. *D. commixta* is a sexual tetraploid with n=82 as described above. So it seems that this hybrid may be formed by a cross between a sexual tetraploid *D. commixta* and an unknown sexual tetraploid or apogamous diploid. The spore of this plant is also abortive.

D.×pseudo-commixta Kurata was proposed by Kurata (1964) for a fern, considered as the hybrid between *D. commixta* Tagawa and *D. pycnopteroides* C. Chr. Cytological investigation of this plant by the author, shows it to be tetraploid hybrid (2n=164) with a meiotic chromosomal arrangement of c. 33 pairs and c. 98 singles during meiosis (Fig. 1-E). *D. commixta* is a sexual tetraploid and *D. pycnopteroides* is an apogamous diploid as described above. Therefore, this hybrid may be formed by a combination of female gamete of *D. commixta* with male gamete of *D. pycnopteroides* as Kurata (1964) described. In addition, this plant shows 16 spore mother cells, but the spore is abortive.

D. monticola C. Chr., from cytological investigation by the author, is a sexual diploid species showing 41 chromosome pairs during meiosis and giving rise to viable 64 spores in a sporangium. This agrees with the previous report by Kurita (1965).

D. sieboldii O. Kuntze, cytologically, is tetraploid with n=82 and sexual with regular sporogenesis as Kurita (1962) reported.

D. hayatai Tagawa is diploid with n=41 and sexual with normal spore formation (Fig. 1-B). This agrees with the previous reports by Mitui (1966) and Kurita (1967).

D. melanocarpa Hayata closely resembles *D. sparsa* O. Kuntze morphologically. According to cytological investigation by the author, it is triploid, showing 123 chromosome pairs during meiosis and apogamous, giving rise to 32 spores in a sporangium (Fig. 2-A). Therefore, this taxon should be given specific status, based on its different chromosome number as compared with *D. sparsa,* having n=82 (Hirabayashi 1966, Kurita 1966). In addition, this plant showed the two phases, namely triploid and diploid phase, in the gametic chromosome number during first meiotic metaphase, as the author (Hirabayashi 1967) described previously on the most of taxa in the section Polysticho-drys H. Ito.

D. yakusilvicola Kurata was proposed by Kurata (1967) for a fern, considered as an intermediate between *D. sparsa* O. Kuntze and *D. sabaei* C. Chr. Cytological investigation by the author showed that this plant is triploid with n=123 and probable apogamous giving rise to 32 spores in a sporangium (Fig. 1-G). Since *D. sparsa* is a sexual tetraploid species (Hirabayashi 1966, Kurita 1966) and *D. sabaei* is a sexual diploid species (Kurita 1962, Hirabayashi 1966), the proposition of Kurata may be supported.

On the following 3 taxa, *D. erythrosora* O. Kuntze var. *koidzumiana* H. Ito, *D. gymnophylla* C. Chr. and *D. sordidipes* Tagawa, it was demonstrated that each of them is a diploid species with n=41 and sexual with normal spore formation by the present study. These results agree with the previous reports by Kurita (1966) for *D. gymnophylla* and by Mitui (1967) for *D. erythrosora* var. *koidzumiana* and *D. sordidipes.*

On the following 5 taxa, *D. kenzoi* Kurata tentative (name), *D. labordei* Ching var. *simasakii* H. Ito form. *paleacea* H. Ito, *D. sacrosancta* Koidzumi, *D. ryo-itoana* Kurata and *D. formosana* C. Chr., the author clarified that them are all apogamous triploid species with n=123, producing 32 spores in a

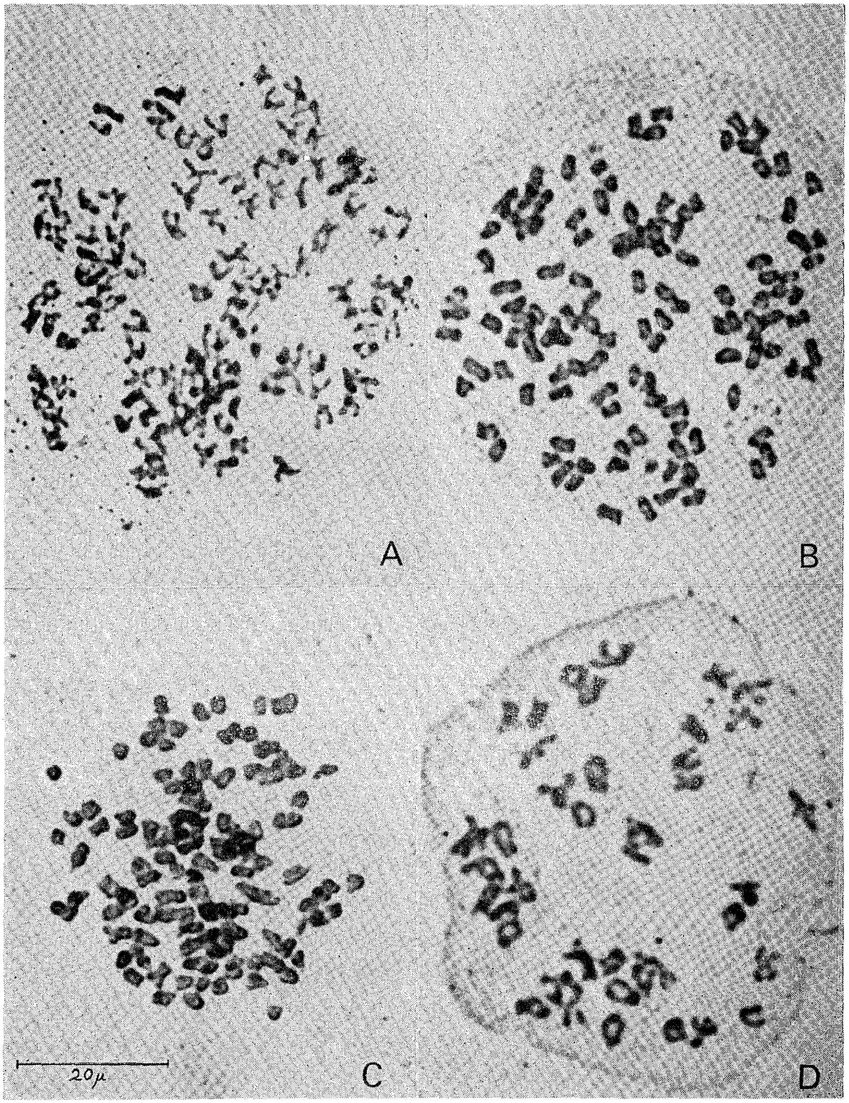

Fig. 2. Photomicrographs of chromosomes at meiosis. A. *D. melanocarpa* Hayata n=123. B. *D. kenzoi* Kurata n=123. C. *D. sacrosancta* Koidzumi n=123. D. *D. austriaca* Woynar n=41.

sporangium (Fig. 2–B, C). In addition, the following 2 plants in these taxa, *D. labordei* Ching var. *simasakii* H. Ito form. *paleacea* H. Ito and *D. sacrosancta* Koidzumi, showed the two phases in gametic chromosome number, namely triploid and diploid phase as described above. For *D. formosana*, Kurita (1967) reported n=123 and suggested apogamous.

D. austriaca Woynar is a sexual diploid species having n=41 and giving 64 spores in a sporangium (Fig. 2–D).

Discussion The first point of discussion is the finding of two possible ancestral diploid species in the subsection Cycadinae H. Ito. This subsection is known to possess an ancestral diploid *D. tokyoensis* C. Chr. In this subsection, two ancestral diploids *D. hangchowensis* Ching and *D. tasiroi* Tagawa (=*D. handeliana* C. Chr.) were newly found by the present investigation. Although *D. hangchowensis* is not reported to hybridize with other taxa until the present, *D. tasiroi* is considered one of putative parent of the hybrid *D.*× *hisatsuana* Kurata. Furthermore, it is noticeable that these ancestral diploids are non-widespread in Japan.

The second point of discussion is the cytological relationships between taxa belonging to the section Eudryopteris H. Ito. A diagrammatic summary of the cytological relationships between the species investigated is given in Fig. 3. On the basis of morphology, seven intermediates are estimated as hybrids between above mentioned putative parents by M. Tagawa (1937), H. Ito (1939) and S. Kurata (1958, 1964, 1967). Cytological evidences support the possibilities of the actual hybridization.

Since the hybrid *D.*× *hisatsuana* Kurata shows 82 singles with no pairing of the chromosome at meiosis, it seems probable that each of *D. lacera* and *D. tasiroi* (=*D. handeliana*), the putative parents, has the different ancestral genomes. The hybrid, *D. kominatoensis* Tagawa also shows 82 singles with little pairing of the chromosomes during meiosis. So it is considered that each of *D. monticola* and *D. tokyoensis*, its putative parents, has the different ancestral genomes. The cytological evidences support that the classificatory treatment by H. Ito, separating these parental species into three subsections, namely the subsect. Dichasium H. Ito, Cycadinae H. Ito and Monticolarum H. Ito, is adequate.

In the subsect. Pycnopteris H. Ito, *D. sieboldii* O. Kuntze is known to hybridize with *D. commixta* Tagawa. However, cytological study of this

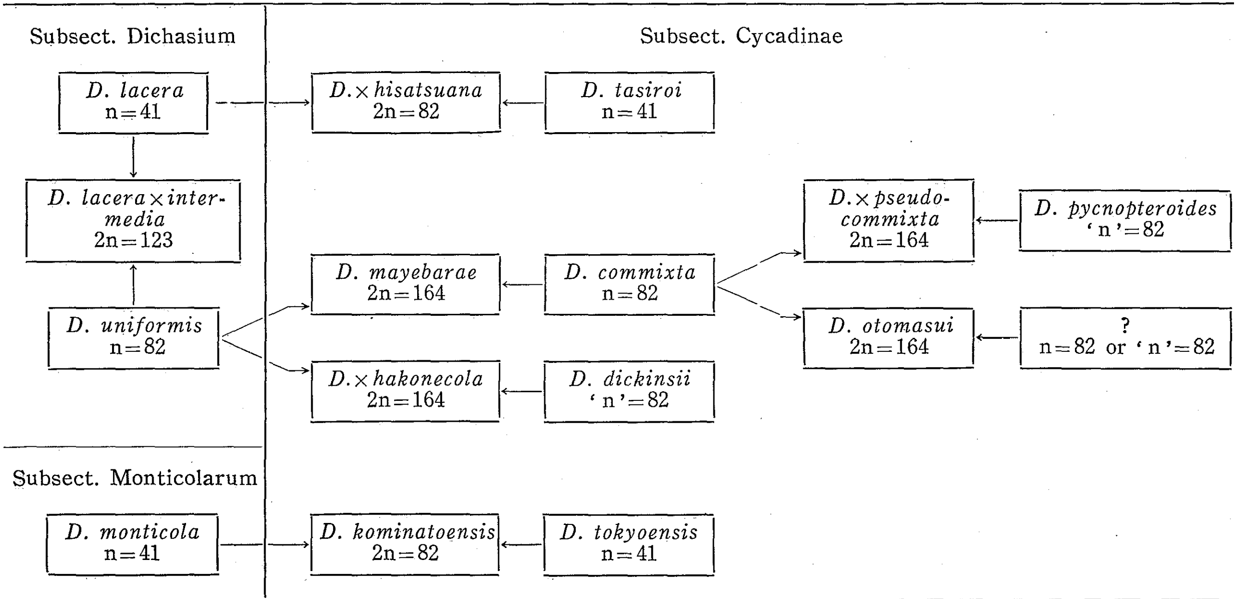

Fig. 3. Cytological relationships between taxa investigated in the sect. Eudryopteris. Morphological relationships was investigated by H. Ito, M. Tagawa and S. Kurata as described in the text.

hybrid, *D.*×*tetsu-yamanakae* Kurata is not given. Since *D. commixta* and *D. uniformis* have a tendency to hibridize not only between them, but with other several taxa, it seems probable that each of them has a common set of chromosomes with others. In the subsect. Dichasium H. Ito, several putative hybrids have been found. Cytological investigations of these hybrids, however, are not yet made, except *D. lacera* O. Kuntze form. *intermedia* H. Ito.

Hence, the relationships between taxa belonging to the sect. Eudryopteris H. Ito remain in future cytogenetic problems. Cytological and morphological comparison of these wild hybrids in Japan with the synthesized hybrids is necessary as S. Walker (1955, 1959, 1961, 1962) has previously made on European and North American species of *Dryopteris.*

The third point of discussion is a problem of apogamous ferns. In the sect. Nephrocystis H. Ito, two apogamous triploid (n=123) ferns, *D. melanocarpa* Hayata and *D. yakusilvicola* Kurata, were found in the present study. According to morphological investigation by Kurata (1967), *D. yakusilvicola* is an intermediate between *D. sparsa* (n=82) and *D. sabaei* (n=41). This suggests that apogamous triploid fern results from cross between a diploid species and a tetraploid species, although further work will solve the problem of origin of apogamous fern.

The sect. Polysticho-drys H. Ito is reported to possess many apogamous triploids. In the present study, four apogamous triploid species were found newly in this sect. Therefore, above all, in the subsect. Erythro-variae H. Ito, cytological analysis of the apogamous triploid species in so-called *D. erythrosora* complex and *D. varia* complex has become more difficult.

On the other hand, apogamous diploid ferns, *D. dickinsii* C. Chr. and *D. pycnopteroides* C. Chr., form a tetraploid hybrid respectively, crossing with a sexual tetraploid species as mentioned above. Besides, Kurata suggested that *D.*×*shibisanensis* Kurata is an intermediate between an apogamous triploid, *D. atrata* Ching and a sexual tetraploid, *D. commixta* Tagawa on the basis of morphology, although this intermediate is not yet investigated cytologically. These fact show that the apogamous fern does not represents an evolutionary terminus.

Walker (1962) investigated the origin of *D. clintoniana* Dowell in North America. According to his cytogenetic studies, this species is a sexual allohexaploid (n=123) and derived from a hybrid between *D. cristata* A. Gray (n=82) and *D. goldiana* A. Gray (n=41) doubling by chromosomes. Since the hybrid, *D. cristata*×*goldiana*, the type specimen of which shows abortive spores, it seems probable that this is not apogamous. Hence, in this case, it is possible that there is no relationship between a sexual hexaploid species and an apogamous triploid species. Further work will clarify this relationship. In fact, in Japan, a sexual hexaploid species in *Dryopteris* is unknown until the present.

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オシダ属に属する 27 種について，その染色体数を調べ，次のような結果を得た。n=41 のものキリシマイワヘゴ，ツクシオオクジャク，タニヘゴ，ミヤマベニシダ，

イヌタマシダ，ホコザキベニシダ，サクライカグマ，ヨゴレイタチシダ，シラネワラビ。

n=82 のものツクシイワヘゴ，オオミツデ，オオクジャクシダ（無配生殖），ワカナシダ（無配生殖）。

n=123 のもの（すべて無配生殖）クロミノイタチシダ，コスギイタチシダ，エンシュウベニシダ，アツギノヌカイタチシダマガイ，オオイタチシダ，オワセベニシダ，タカサゴシダ。

2n=82 の雑種ヒサツオオクジャク，タニヘゴモドキ。

2n=123 の雑種アイノコクマワラビ。

2n=164 の雑種ハコネオオクジャク，イワヘゴモドキ，ヤタケイワヘゴ，オオスミイワヘゴ。

以上の結果から，次のようなことがいえよう。

1) イワヘゴ亜節において，すでに報告されたイワヘゴの他は，キリシマイワヘゴとツクシオオクジャクの祖先型二倍性種が発見された。

2) イワヘゴ亜節における雑種シダの数種について，その雑種性が細胞学的にも裏付けされた。

3) オシダ節を数亜節に分けることの妥当性は細胞学的にも支持される。

4) コスギイタチシダ（n=123, 無配生殖）がミヤマイタチシダ（n=41）とナガバノイタチシダ（n=82）の交雑によって生じた可能性が細胞学的にも裏付けされたことは，無配生殖性シダの起源を考えるのに示唆に富む。

5) 無配生殖するシダであるオオクジャクシダ，ワカナシダ等が他の種と交雑して雑種をつくりうる可能性があることは，無配生殖性シダが進化の終点でないことを示唆する。

□徳田御稔：**生物地理学** 28年前に出版された日本生物地理学を，復刻する目的で計画されたものであるが，その内容は著者の研究内容の深まりを反映して，全く異ったものとなっている。ネズミ類の進化を中心としているが，方法論の上から重要な問題を多く含んでおり，植物地理学に関心のある者は一読する必要がある。生物地理学の基礎としては，生きている状態の種を環境との，また系統分類との関連において進めるのが大切であり，近代的の名のもとに提唱された生態地理学は，むしろ近代の名にふさわしくないものであるとしているのは，今後の生物地理学の方向にとって重要な問題を提供している。ただ著者の植物群落は社会構造をもたないという考えかたには疑問をもつ。私は群落は種が生活をするために作りだしている基盤であり，異る種どうしで作られる複合的な社会とみるからである。200頁，築地書館，1969年，980円。

（山崎 敬）